Vaccinium species of section *Hemimyrtillus*: their value to cultivated blueberry and approaches to utilization[1]

M.K. Ehlenfeldt and J.R. Ballington

Abstract: The primary gene pool of *Vaccinium* species used by breeders has traditionally been the North American *Vaccinium* species in section *Cyanococcus*. Blueberries in commercial production represent several *Vaccinium* species and ploidies. Moreover, significant use has been made of the secondary gene pool of *Vaccinium*, especially in the development of southern highbush cultivars. Section *Hemimyrtillus* represents species that are part of the tertiary gene pool of *Vaccinium*. Two species of section *Hemimyrtillus*, native to the Portuguese islands of Madeira (*Vaccinium padifolium* Smith) and the Azores (*Vaccinium cylindraceum* Smith), have features of notable value to conventional blueberry development such as upright structure, strong growth, abundant flowering and fruiting, good self-fertility, acceptable fruit quality, inflorescence structure suited to mechanical harvesting, and repeat flowering. *Vaccinium cylindraceum* is deciduous, whereas *V. padifolium* is evergreen. *Vaccinium arctostaphylos* L., a native of the Caucasus region, is closely allied to *V. padifolium*, hybridizes freely with it, and has many similar characters, but with the valuable addition of greater cold hardiness. Initial progress has been made at incorporating these species into forms compatible with *Vaccinium corymbosum* L. based blueberry cultivars, and further evaluations are being made of both parental material and the derived hybrids.

Key words: Vaccinium padifolium, *Vaccinium cylindraceum*, *Vaccinium arctostaphylos*, *Vaccinium smallii*, *Vaccinium yakushimense*, *Vaccinium hirtum*.

Résumé : Le pool de gènes primaires des *Vaccinium* spp. utilisé par les améliorateurs comporte traditionnellement des espèces de *Vaccinium* nord-américaines de la section *Cynococcus*. Les bleuets commerciaux englobent plusieurs espèces et ploïdies. De plus, on a fait une utilisation significative du pool de gènes secondaires des *Vaccinium*, surtout pour le développement des cultivars de bleuets en corymbe méridionaux. Deux espèces de la Section *Hemimyrtillus*, natives des iles portugaises de Madère (*Vaccinium padifolium* Smith) et des Açores (*Vaccinium cylindraceum*), possèdent des caractéristiques de valeur appréciable pour le développement des bleuets conventionnels, parmi celles-ci : structure dressée, croissance robuste, floraison et fructification abondantes, bonne autofécondation, qualité de fruit acceptable, structure de l'inflorescence se prêtant bien à la récolte mécanique, et floraison répétitive. Une de ces espèces est décidue et l'autre sempervirente. Le *Vaccinium arctostaphylos* L. une espèce native du Caucase, se rapproche étroitement du *V. padifolium*, s'hybride facilement avec cette dernière et possède plusieurs caractéristiques similaires, avec en plus une résistance au froid. Des progrès initiaux ont été obtenus dans l'incorporation de ces espèces sous des formes compatibles avec les cultivars de bleuets basés sur le *Vaccinium corrymbosum* L. et l'on conduit présentement d'autres évaluations à la fois sur le matériel parental et les hybrides dérivés.

Mots-clés : Vaccinium padifolium, *Vaccinium cylindraceum*, *Vaccinium arctostaphylos*, *Vaccinium smallii*, *Vaccinium yakushimense*, *Vaccinium hirtum*.

[Traduit par la Rédaction]

Introduction

Blueberries (family Ericaceae, species *Vaccinium*, commonly section *Cyanococcus*) are a diverse taxonomic group. Blueberries currently in commercial production represent several *Vaccinium* species and ploidies: *Vaccinium angustifolium* Aiton (4*x*; lowbush blueberry), *Vaccinium corymbosum* L. (4*x*; highbush blueberry), and *Vaccinium corymbosum* forma *ashei* (6*x*; rabbiteye blueberry). As such, these three types may be considered the primary gene pool of blueberry. Two other commercial types of blueberry are mixtures of species: half-highbush blueberry cultivars have been produced by hybridization of *V. corymbosum* (4*x*) and *V. angustifolium* (4*x*) and retain a significant but variable percentage

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contribution from each species; southern highbush cultivars have been developed by the introgression of the low-chilling-requirement species *Vaccinium darrowii* Camp (2*x*) into *V. corymbosum* (4*x*) at a contribution level averaging about 25%. Several additional species from the secondary gene pool of blueberry, among them, *Vaccinium corymbosum* forma *elliottii* (2*x*), *Vaccinium corymbosum* forma *constablaei* (6*x*), and *Vaccinium tenellum* Aiton (4*x*), have also contributed small amounts of germplasm to named blueberry cultivars.

Blueberry species are rather promiscuous, and as a result, most of the utilization of the previously mentioned species has been relatively straightforward. Diploid species often produce unreduced gametes at low frequencies that have allowed their utilization with cultivated tetraploid partners (Ortiz et al. 1992), and tetraploid and hexaploid species typically can hybridize freely. Often the greatest difficulty has been lowered fertility owing to the production of odd-ploid hybrids (a particular problem with pentaploids from $6x \times 4x$ crosses). The ability to transfer germplasm via conventional crosses led Hall and Galletta (1971) to hypothesize a highly conserved basic genome in the genus *Vaccinium*. As a result, a problem of equal or greater importance in the utilization of exotic species hybrids is the recovery of fruit morphology that is neither too small nor too dark to meet commercial standards.

Section *Hemimyrtillus* and its species

Sam P. Vander Kloet of Acadia University, Nova Scotia, Canada, a good friend and one of the world's foremost *Vaccinium* taxonomists, studied the species of section *Hemimyrtillus* as extensively as anyone working with *Vaccinium* species. In this paper, we draw on many of his observations on species of section *Hemimyrtillus*. Several of the specimens of *Vaccinium padifolium* Smith and *Vaccinium cylindraceum* Smith used in this study, which are part of the US germplasm collection (Corvallis, Oregon), were collected by S.P. Vander Kloet.

Vander Kloet and Dickinson (1992) considered the existing species of section *Hemimyrtillus* to be the remnants of a once much more widely distributed taxon. Today, six species are considered to occupy section *Hemimyrtillus*, and three of these are found in very limited localities. The species and their ranges are as follows: *V. cylindraceum* (the Azores, Portugal), *V. padifolium* (Madeira Islands, Portugal), *Vaccinium arctostaphylos* L. (Caucasus Region), *Vaccinium smallii* Gray (Korea, Japan, and Russia), *Vaccinium yakushimense* Makino (Yakushima Island, Kyushu, Japan), and *Vaccinium hirtum* Thunb. (Japan and South Korea) (Fig. 1).

An easily recognizable morphological feature that unifies *Hemimyrtillus* is the set of paired prophylls covering perenniating buds. To quote Vander Kloet and Dickinson (1992): "Section *Hemimyrtillus* shares with sections *Myrtillus*, *Macropelma*, and *Oxycoccoides* the apomorphic character of buds composed of two partially fused prophylls (hence its name), but differs in having its flowers borne on racemes and having pedicels articulated with the calyx tube. In sections *Myrtillus*, *Macropelma*, and *Oxycoccoides* the flowers are borne singly in leaf axils and the pedicels are continuous with the calyx tube." In section *Hemimyrtillus*, the fused prophylls result in a distinctive, narrow bud, looking much like the nail of an animal claw (Fig. 2). S.P. Vander Kloet and T.A. Dickinson also note that among species of section *Hemimyrtillus*, twigs are typically smooth or pitted (but not verrucose). In an effort to resolve earlier disagreements about the taxonomy of the species of section *Hemimyrtillus*, S.P. Vander Kloet and T.A. Dickinson conducted a principal coordinate analysis of 26 quantitative and qualitative characters of 14 different species of sections *Cyanococcus* and *Hemimyrtillus*. They found section *Hemimyrtillus* to be distinct from species of section *Cyanococcus* (cluster-forming blueberries) and concluded that the western *Hemimyrtillus* species (*V. cylindraceum* (Azores), *V. padifolium* (Madeira), and *V. arctostaphylos* (Caucasus)) could be shown to be distinct from the Northeast Asian *Hemimyrtillus* species. A more recent DNA-based evaluation of numerous *Vaccinium* species by Powell and Kron (2002) using both nuclear and chloroplast markers supported these differences and suggested that the Northeast Asian *Hemimyrtillus* (*V. smallii*, *V. yakushimense*, and *V. hirtum*) and the "Tethyan" *Hemimyrtillus* (*V. cylindraceum*, *V. padifolium*, and *V. arctostaphylos*) each form well-supported but separate clades, which led them to suggest that the Northeast Asian species should be removed from section *Hemimyrtillus* (Fig. 3). These species appear more closely related to sections *Praestantia* and *Oxycococcoides*. Nonetheless, Vander Kloet and Dickinson (2009) commented "… it is premature to dismember this section especially since bud development and inflorescence development is similar for both groups, and … [since] … molecular data [is] available for only a fraction of the species, … the overall topology of the *Vaccinium* phylogeny is still in flux."

The Tethyan *Hemimyrtillus* have many desirable features from a breeder's point of view. These are physically robust species in which nature has, in a sense, already done considerable prebreeding. The following summation is taken largely from Vander Kloet and Dickinson (1992), and it is supplemented with other sources and our personal observations.

Vaccinium cylindraceum — This species is also known as the Uva de Serra (Berry of the Mountains) and (or) the Azore blueberry. *Vaccinium cylindraceum* is found natively on Faial, Pico, São Miguel, and Terceira Islands in the Azores on volcanic slopes of 350–1550 m. It is associated with *Myrica*, *Erica*, and *Laurus* at lower elevations, and it is often found in *Calluna* heaths at higher elevations. Plants are deciduous, tree-like, and 1–4 m tall. Prominent thickening at nodes may occur on older woody material of *V. cylindraceum*. Plants are drought-tolerant and succeed in neutral soils that are not too heavy (Trehane 2004). Leaves are variable, with some clones possessing relatively large, lance-shaped leaves and others possessing smaller leaves with a pronounced serrated edge. The leaves are tough, semi-glossy and have a distinct net-like patterning. Plants flower in profusion, and both flowers and ripe fruit can be present on the plant simultaneously (Trehane 2004). Flowers are cylindrical and elongated, hence the name *V. cylindraceum*. Flowers are typically deep pink at anthesis, fading to cream or white as they age. Fruit is medium-blue and ovate. The berry is the native food of the endangered Azores Bullfinch (*Pyrrhula murina*), which is typically found at higher elevations in the volcanic mountains at about 1000–1500 m. European blueberry rust is present on São Miguel Island in the Azores, and *V. cylindraceum* growing there appear susceptible (Hummer et al. 2009). Our limited observations with greenhouse-grown plants suggest they

Fig. 1. Distribution of species of section *Hemimyrtillus* (after Vander Kloet and Dickinson 1992).

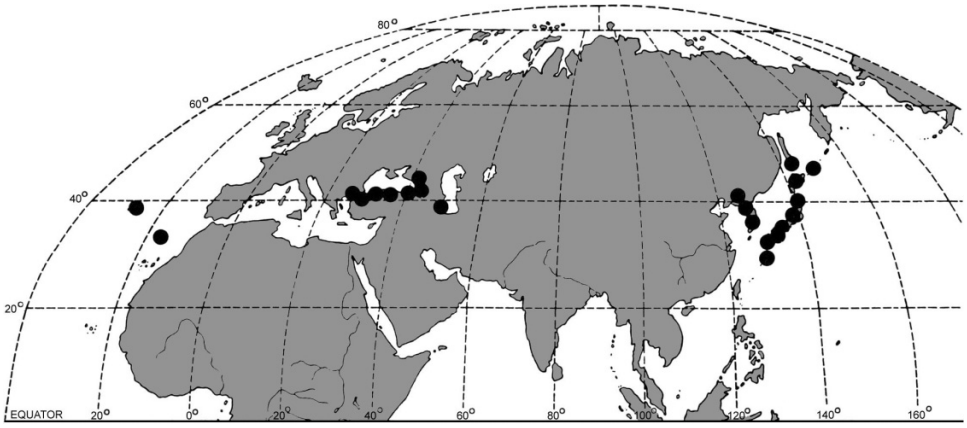
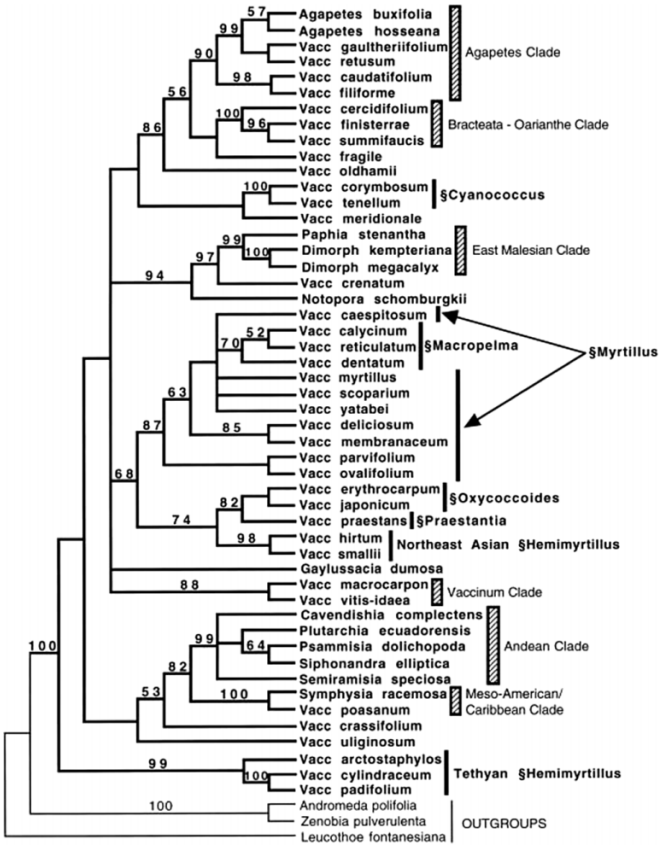


Fig. 2. *Hemimyrtillus* prophyll structure.

Fig. 3. DNA-based taxonomic tree of *Vaccinium* species. Strict consensus of 120 most parsimonious trees found in a combined analysis of nrITS, *matK*, and 5′ *ndhF* sequences of 50 species from tribe Vaccinieae and three outgroups. Bootstrap values greater than 50% are shown above the branches (reproduced from Powell and Kron 2002 by permission of the American Society of Plant Taxonomists).

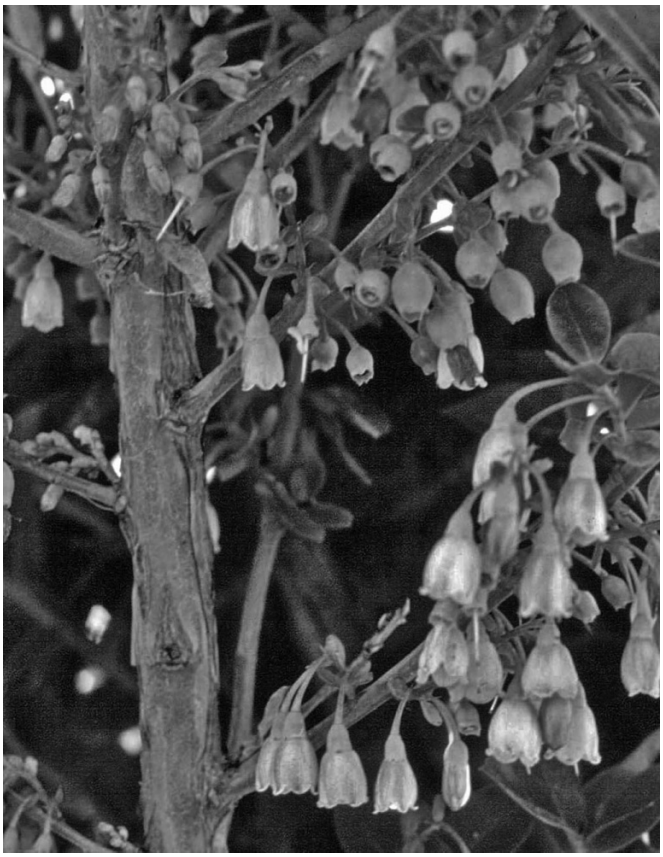


may be scale prone, with prophylls being a spot under which scale insects can take refuge and overwinter. The ploidy level of *V. cylindraceum* is unknown.

Vaccinium padifolium — This species known as the Madeira whortleberry was first collected in 1777 by Francis Masson, an early plant explorer for the Royal Kew Gardens who transmitted specimens to Linneaus. Early descriptions of *V. padifolium* were published in Ree's Cyclopædia (Smith 1817), in *Enumeratio Plantarum Horti Botanici Berolinensis* (as *Vaccinium maderense*) (Link 1821), and later in Curtis's Botanical Magazine (Hooker 1893). *Vaccinium padifolium* is native only to the Madeira Islands, and it is typically found in subalpine shrubberies, degraded pastures, draws and edges of coniferous woods, and pine barrens at altitudes of 1220–1700 m. Plants are bushy to tree-like and may be 1–4 m tall. Under native conditions, plants possess an evergreen habit. In general, our specimens have tough, semi-glossy leaves with a netted appearance similar to the larger-leaved clones of *V. cylindraceum*. Plants flower profusely and produce creamy, pink-tinged, bell-shaped flowers that give rise to medium-blue, ovate fruit. Quite notably, both flowers and fruit can appear on the plant simultaneously (Fig. 4). Like *V. cylindraceum*, the ploidy level is unknown, and the authors' observations suggest *V. padifolium* may be scale prone.

Vaccinium arctostaphylos — The earliest description of *V. arctostaphylos* was published in Curtis's Botanical Magazine (Anonymous 1806). *Vaccinium arctostaphylos* is a dis-

Fig. 4. A stem of *Vaccinium padifolium* showing profuse flowering and the simultaneous presence of flowers and developing fruit.



junct species, with populations in Bulgaria, Turkey, and Anatolia as well as a relict population near the Caspian Sea. It is a mesophytic understory shrub found in open beech or oak woods as well as in a variety of coniferous stands. It is typically found on mountain slopes of 500–2400 m, and it is often associated with *Rhododendron* and *Erica* shrubberies. Plants are deciduous, 1–6 m tall, and have a relatively smooth bark. The selections of *V. arctostaphylos* we have observed have finer leaves than the previous two species, but the texture can vary considerably. Some of our selections appear susceptible to an undetermined foliar blight. Flowering is less prolific than the previous two species, but like them, the plants may have a second flush of flowers (Trehane 2004). Flowers normally have a distinct red coloration at anthesis and fade to shades of pink and cream. Fruit is black, round, and glossy. Plants have been observed to be hardy to –15 °C (Trehane 2004). Darrow et al. (1944) determined a single specimen of *V. arctostaphylos* to be 4*x*.

Under our conditions, the Northeast Asian *Hemimyrtillus* (*V. hirtum*, *V. yakushimense*, and *V. smallii*) are much less robust (although *V. smallii* may reach 1–3 m under natural conditions) and flower only irregularly. They also tend to have inflorescences with only a few flowers (1–3 flowers) (Vander Kloet and Dickinson 1992). Under native conditions, these species are found either as epiphytes (specifically *V. yakushimense*) or are found growing on stumps and rotting logs. Because of these limitations, these species receive only limited treatment here. Readers may refer to Vander Kloet and Dickinson (1992) for a more extensive review of these species.

Utilization value of the Tethyan *Hemimyrtillus* species

The species of section *Hemimyrtillus* are more distantly related to commercial blueberry than many of the species previously utilized in breeding, and almost certainly would be considered to lie in the tertiary gene pool. Nonetheless, our rationale in working to incorporate germplasm from species in this section lies in the desirable characters these species have for mechanical harvesting and commercial production.

Vaccinium cylindraceum has a long inflorescence, primarily attributable to its long pedicels, a trait that may be of considerable value for mechanical harvesting, if it can be incorporated into commercial blueberries. Our observations also suggest that fruit of *V. cylindraceum* separate reasonably from the pedicels (also needed for mechanical harvest). The fruit quality of *V. cylindraceum* is acceptable but undistinguished. *Vaccinium cylindraceum* has a long style that might not be successfully traversed by pollen from other species, and thus for incorporation purposes it is likely to be most successful as a male in crosses. *Vaccinium cylindraceum* is desirable for its profuse flowering with high numbers of flowers per bud. It is also notable for its repeat flowering, which may allow multiple cropping or continuous cropping. Other useful traits include its general vigor, large mature plant size, excellent fertility, good fruit size, and general self-fruitfulness.

Vaccinium padifolium is similar to *V. cylindraceum* in most respects, but as noted previously, it is an evergreen. Its evergreen nature may be a useful trait under some conditions, but it may also present management problems in terms of physiology and (or) allowing the plants to be an insect or pathogen reservoir under field conditions. Like *V. cylindraceum*, *V. padifolium* is notable for its profuse flowering, repeat flowering, and its high numbers of flower buds located on both young and old wood. It too is valuable for its vigor, its large mature plant size, excellent fertility, good fruit size, and general self-fruitfulness.

Vaccinium arctostaphylos is a valuable complement to the other two species. It has greater cold hardiness, and it appears to have a tolerance to upland soils. It also has the potential to be more robust (i.e., taller) than the other two species. Its fruit is black, and its fruiting is less prolific than *V. cylindraceum* and *V. padifolium*, but all indications are that it will freely recombine with these species. Together, the three species represent a considerable range of diverse and desirable germplasm.

The earliest reported attempt to use these species in the development of cultivated blueberry was Darrow and Camp (1945) who reported making the cross *Vaccinium australe* (syn. *V. corymbosum*) × *V. arctostaphylos*. They did not however, subsequently report that any hybrids had been produced. We are not aware of any further reports by G.M. Darrow of hybrids or advanced selections that resulted from this cross.

Beyond this, the Tethyan *Hemimyrtillus* species have a modest track record as ornamentals. An ornamental hybrid of *V. cylindraceum* × *V. arctostaphylos* named 'Prince Charming' was developed by B. Starling, of Exeter, England (Trehane 2004). Similarly, the cultivars 'Tom Thumb' and 'Tinkerbell', a dwarf and extra-dwarf ornamental, respectively, of *V. cylindraceum* were also selected by B. Starling (Trehane 2004).

We review here the previous and ongoing hybridization efforts with these species and discuss the potential of hybrids derived thus far.

Material and methods

Using traditional emasculation and pollination procedures, Ballington (2000) at North Carolina State University (NCSU) made numerous intersectional crosses with *V. cylindraceum* that incorporated this germplasm with both 2*x* and 4*x* germplasm. Viable hybrids, when feasible, were planted into field plots at NCSU research stations to observe performance of hybrids under field conditions. J.R. Ballington used several viable first-generation hybrids to generate second-generation hybrids. Several of these hybrids were also grown under field conditions to observe their performance and to subjectively evaluate the inheritance of section *Hemimyrtillus* traits. Beginning in 2009, and using similar practices, but without emasculating, M.K. Ehlenfeldt with the US Department of Agriculture, Agricultural Research Service (USDA-ARS) at Chatsworth, New Jersey, made both intrasectional and intersectional crosses with *V. padifolium*, *V. cylindraceum*, and *V. arctostaphylos*. A small number of crosses were also made with *V. smallii*. At writing, these sets of hybrids have only been observed as seedlings and only under greenhouse conditions.

Results

Crosses undertaken with section *Hemimyrtillus* species were successful in several different combinations. As noted previously, section *Hemimyrtillus* species appear to be exceptionally self-fertile, and the intrasectional hybridizations among these species appeared to be accomplished quite easily. Verification of hybridity for many of these putative intrasectional hybrids is ongoing. Intrasectional hybrids had adequate but variable vigor. Intrasectional hybrids involving *V. cylindraceum* (much like pure *V. cylindraceum* seedlings) appear to have a prolonged period of slow juvenile growth (M.K. Ehlenfeldt, personal observation).

Intersectional hybrids (where confidence in hybridity is high) were generally produced at very low frequencies and had mixed results with respect to the vigor and vitality of the putative hybrids. Among these species, *V. cylindraceum* appeared to combine less successfully with species outside of its section than did *V. padifolium*. An elaboration of both intrasectional and intersectional hybrids follows.

Primary hybrids

§ Hemimyrtillus × *§ Hemimyrtillus* hybridizations

Vaccinium padifolium × *V. arctostaphylos* (USDA) — This cross was easily accomplished and produced an abundance of seedlings. It is notable that this cross mirrored that which produced the ornamental 'Prince Charming'. The plants appeared to be obvious hybrids with intermediate features. At the time of writing, however, these putative hybrids had not yet grown large enough to flower. Assuming that G.M. Darrow's determination of *V. arctostaphylos* as a tetraploid is correct, this hybridization success suggests that *V. padifolium* may be tetraploid as well.

Vaccinium padifolium × *V. cylindraceum* (USDA) — This cross produced ample amounts of what appear to be hybrids, but at this point most exhibit less vigor than one might expect, based on their parentage; none has yet grown large enough to flower.

§ Cyanococcus (2*x*) × *§ Hemimyrtillus*

Vaccinium darrowii (2*x*; NC 86-4-5) × *V. cylindraceum* (NC 3730) (NCSU) — This cross yielded five seedlings. One seedling, NC 3865, was determined to be tetraploid, presumably derived from a 2*n* egg of *V. darrowii* and a 2*x* male gamete from *V. cylindraceum* (somatic ploidy level unknown). This hybrid was fertile and moderately vigorous. Inflorescence and leaf characteristics of this hybrid are intermediate to the parents (Fig. 5). The other four hybrid seedlings were weak, declined in vigor over several years, and died.

§ Polycodium (2*x*) × *§ Hemimyrtillus*

Vaccinium stamineum (2*x*; NC 84-1-2) × *V. cylindraceum* (NC 3730) (NCSU) — This cross yielded two very weak seedlings that did not survive past their second year.

§ Cyanococcus (4*x*) × *§ Hemimyrtillus*

Vaccinium corymbosum (4*x*; NC 1872) × *V. cylindraceum* (NC 3730) (NCSU) — This cross yielded four seedlings that were established in the field at Jackson Springs, North Carolina. All were relatively weak, but two are still alive after 6 years in the field. None of these seedlings have produced flowers or fruit to date.

Vaccinium angustifolium (4*x*) × *V. padifolium* (USDA) — Numerous putative hybrids were produced from this cross, but their veracity is as yet undetermined. Plants appear much more like pure *V. angustifolium* than they do hybrids at this point. This cross was made because the *V. angustifolium* clone expressed a fall-flowering character (not uncommon in *V. angustifolium*) much like the indeterminate flowering of *V. padifolium*.

Vaccinium padifolium × *V. corymbosum* (4*x*; southern highbush) (USDA) — At a low frequency, these crosses have yielded what appear to be two successful hybrids. The more vigorous of the two (US 1896) has foliage of intermediate appearance, with the netted leaf surface of *V. padifolium* but leaf shape intermediate to the two parents (Fig. 6). The second and slightly less vigorous clone (US 1897), also appears to be a hybrid but appears more highbush-like. Similar to the previous combination, these specific crosses were made because the southern highbush clones used as males expressed a fall-flowering character much like the indeterminate flowering of *V. padifolium*.

§ Cyanococcus (6*x*) × *§ Hemimyrtillus*

Vaccinium corymbosum forma *ashei* (6*x*) derivative × *V. smallii* (USDA) — A 6*x* hybrid composed of germplasm from *V. corymbosum* forma *ashei* (6*x*), *V. corymbosum* forma *constablaei* (6*x*), *V. corymbosum* (4*x*), and *V. darrowii* (2*x*), which was the product of a cold-hardy rabbiteye development program, was pollinated with a small amount of *V. smallii* pollen that was available in 2010. Thirty-five (35) pollinations produced 33 fruit (4 medium-sized and 29 small-sized). Seven seed judged to be potentially viable were produced. From these, five putative hybrids (based on observations of

Fig. 5. Leaves of *Vaccinium cylindraceum* and the *Vaccinium darrowii* × *V. cylindraceum* hybrid (NC 3865).

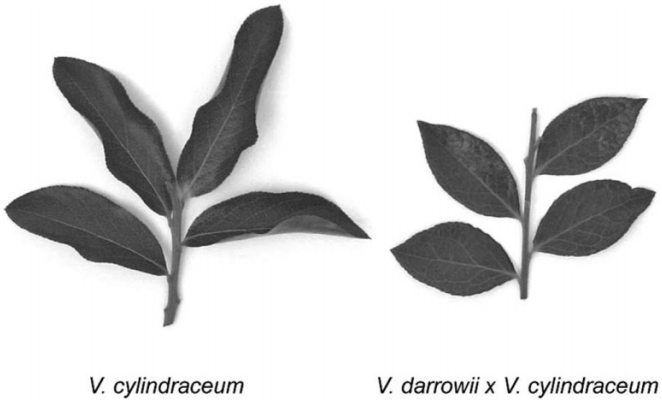
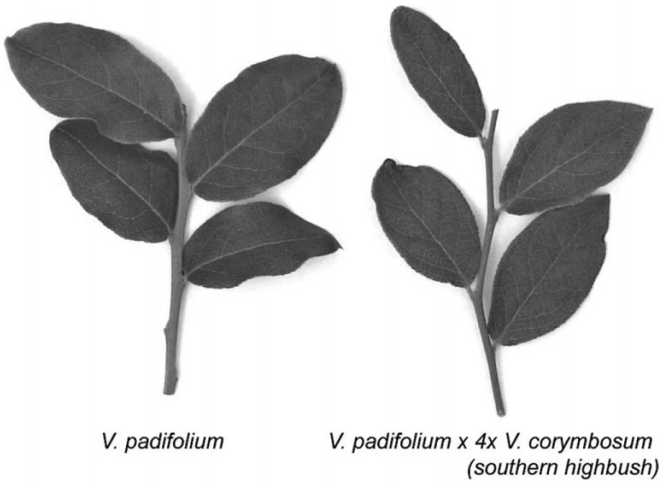


Fig. 6. Leaves of *Vaccinium padifolium* and the *Vaccinium padifolium* × *V. corymbosum* (4*x*) hybrid (US 1896).



seedling morphology) have been produced. These hybrids appeared to be slow to germinate, and they may have derived from substandard-sized seed; nonetheless, they seem to be of average vigor. The ease of producing these hybrids with such a modest number of pollinations represents an unexpected success in introgressing such germplasm.

Second-generation hybrids

§ Cyanococcus × *§ Hemimyrtillus*

(*Vaccinium darrowii* × *V. cylindraceum*) (4*x*; NC 3865) × *V. corymbosum* (4*x*) (NCSU) — The tetraploid hybrid (NC 3865) was crossed to two tetraploid southern highbush genotypes, 'Legacy' and NC 2856 (a complex hybrid involving five *Vaccinium* species). The backcross seedlings in both progenies were uniformly very early flowering, and hence, subject to frost damage. They were also fertile and quite variable in vigor with dull to shiny black fruit. One BC_2 progeny is currently being grown for evaluation in the field. Fruit of *V. cylindraceum* is ovate, and this morphology is expressed to some degree in this and other *V. cylindraceum* crosses.

§ Cyanococcus × *§ Hemimyrtillus* × *§ Pyxothamnus*

(*V. darrowii* × *V. cylindraceum*) (4*x*; NC 3865) was also crossed to NC 3048 (a 4*x* hybrid generated from ((*V. corymbosum* (2*x*) × *V. darrowii*) × *V. darrowii*) (2*x*; NC 2267) × *V. ovatum* (2*x*; BLJ-13-6)) (NCSU) — From this cross, five random F_1 were intercrossed to produce an F_2 progeny cohort. Ninety-seven F_2 seedlings were established at Jackson Springs, North Carolina, and all the seedlings appeared to be fertile. Very early bloom predominated along with black to dull-black fruit. However, there was segregation for glaucous leaves and blue fruit, and these two traits appeared to be linked. Several selections from this F_2 progeny are being evaluated as potential ornamental cultivars.

Discussion

The intrasectional crosses among species of section *Hemimyrtillus* were quite easily made and several progeny families had plentiful offspring. This suggests these species are all compatible and exist at the same ploidy level. By contrast, and not surprisingly, the intersectional crosses were mostly difficult crosses with high numbers of pollinations yielding few progeny. Crosses of diploid *V. darrowii* × *V. cylindraceum* yielded a verified tetraploid hybrid, suggesting either bilateral sexual polyploidy (if both are diploids) or the functioning of a 2*n* egg (if *V. cylindraceum* is tetraploid). The other hybrids of diploid *Cyanococcus* × *Hemimyrtillus* were weak, and ploidy was not determined. Crosses of tetraploid *Cyanococcus* × *Hemimyrtillus* were marginally easier to accomplish and appear to produce viable hybrids, sustaining the idea that species of section *Hemimyrtillus* are likely tetraploid.

Amongst the crosses overall, those with *V. cylindraceum* appeared to be somewhat weaker, although this conclusion is based on a limited parental base and a limited selection of offspring. In contrast, *V. padifolium* appeared to have better combining ability, producing many vigorous, putative hybrids with *V. angustifolium* and two strong hybrids with *V. corymbosum* (4*x*) germplasm.

Thus far, the second-generation hybrids produced with species of section *Hemimyrtillus* have utilized only *V. cylindraceum* germplasm. The observed hybrids exhibit good fertility, but they are early flowering and often sustain frost damage. Early flowering is not, however, an insoluble problem, as cultivated germplasm with slow deacclimation and late flowering is known. Success with these hybrids may depend on finding the correct intermediate parent to enhance their local environmental adaptation.

Several questions exist for the future utilization of this material. (*i*) What are the ploidy levels of the various species? This question has an impact on how these plants might be crossed initially, as well as ramifications on what might be expected in subsequent segregating progeny. J.R. Ballington assumed *V. cylindraceum* to be 2*x* and M.K. Ehlenfeldt assumed the same for *V. padifolium*, but our cross results have called this (perhaps naïve) assumption into question. The cross *V. padifolium* × *V. arctostaphylos* was made very easily. If *V. arctostaphylos* is 4*x*, as G.M. Darrow determined, is it likely that *V. padifolium* is also 4*x*? (*ii*) Will intrasectional *Hemimyrtillus* hybrids be more useful than pure species in crossing to *V. corymbosum*, making hybrids with desirable characteristics? The diversity of germplasm, as well as the fact that hybrids have been produced amongst the three

species of section *Hemimyrtillus*, suggests that it might be possible to exercise considerable selection for adaptive and fruiting characteristics before incorporating this material into more conventional germplasm. (*iii*) Will it be easy to recover or maintain desired traits in offspring? At this point little is known about the expression of section *Hemimyrtillus* genes in mixed hybrids or the subsequent inheritance of these traits. Further evaluations of these breeding materials should do much to begin to answer these questions.

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